Full tree resolution of *Polyplectron* Temminck, 1813, confirms species status of Hainan *P. katsumatae* Rothschild, 1906, and Bornean Peacock-Pheasants *P. schleiermacheri* Brüggemann, 1877

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Summary.—Additional molecular (cytochrome-*b*, D-loop and OvoG) sequences have permitted resolution of a phylogenetic tree for all eight taxa of peacock-pheasants *Polyplectron* Temminck, 1813. This confirms previous work indicating that Hainan Peacock-Pheasant *Polyplectron katsumatae* Rothschild, 1906, and Bornean Peacock-Pheasant *P. schleiermacheri* Brüggemann, 1877, are well-differentiated species, a conclusion further supported by plumage, morphology and, in the case of *P. schleiermacheri*, vocalisations. The tree confirms that *P. katsumatae* is one of a cluster of species geographically peripheral to, and derived from, a widespread mainland Asian ancestor that is today represented by *P. bicalcaratum*, and that these two species show greater genetic divergence than exists between Grey *P. bicalcaratum* and Sumatran *P. chalcurum* or Mountain Peacock-Pheasants *P. inopinatum*.

For more than a decade there has been renewed interest in the taxonomy (Zheng 2002, Madge & McGowan 2002, Penhallurick & Walters 2005), nomenclature (Dickinson 2001) and systematics (Kimball *et al.* 2001) of taxa in the genus of peacock-pheasants *Polyplectron* Temminck, 1813. At species level two key questions have been whether the taxon *katsumatae* Rothschild, 1906, from Hainan is specifically distinct from Chinese mainland Grey Peacock-Pheasant *P. bicalcaratum* (Linnaeus, 1758) and whether *schleiermacheri* Brüggemann, 1877, from Borneo is specifically distinct from Malaysian Peacock-Pheasant *P. malacense* (Scopoli, 1786) of the Malay Peninsula.

Bornean Peacock-Pheasant *P. schleiermacheri* was accepted as a species by Beebe (1922), Peters (1934), Inskipp *et al.* (1996), Johnsgard (1986, 1999), Sibley & Monroe (1990), MacKinnon & Phillipps (1993), McGowan (1994), Smythies (1999), Dickinson (2003), Myers (2009) and Phillipps & Phillips (2009). It was reduced to a subspecies of *P. malacense* by Delacour (1951), and this was accepted by Smythies (1957, 1981) and Hennache & Ottaviani (2006).

Hainan Peacock-Pheasant *P. katsumatae* was first described as a species, and authors who have retained it at this rank include Beebe (1922), Inskipp *et al.* (1996), MacKinnon & Phillipps (2000), Madge & McGowan (2002), Zheng (2002) and Liang & Zhang (2011). Peters (1934) was the first author to treat it as a subspecies of *P. bicalcaratum*, while those who have maintained it at subspecies level include Delacour (1951), Meyer de Schauensee (1984), Johnsgard (1986, 1999), Cheng (1987), Sibley & Monroe (1990), Gao (1991, 1999), McGowan (1994), Li (1996, 2004), Dickinson (2003) and Hennache & Ottaviani (2006). Chang *et al.* (2008), who obtained cytochrome-*b* and OvoG sequences from nine individual *katsumatae* and six *bicalcaratum*, found the differences sufficient to recognise them as species and, more significantly, found that they are not each other's closest relatives, being interpolated in phylogenetic estimates by Mountain Peacock-Pheasant *P. inopinatum* (Rothschild, 1903) from the Malay Peninsula.

Collar (2009) critiqued the paper by Chang *et al.* (2008), re-examined the type series of *P. katsumatae* in the American Museum of Natural History, New York (AMNH) and supported species-level recognition for this taxon based on criteria advocated by Tobias *et al.* (2010). He found it difficult to accept that *P. bicalcaratum* could be more closely related to the biogeographically distant *P. inopinatum* than to the 'adjacent' *P. katsumatae*. Collar (2009) also found it difficult to accept that the strongly distinct *P. inopinatum* is phylogenetically interpolated between *P. bicalcaratum* and *P. katsumatae* because the two latter taxa are more similar in their plumage. Kimball *et al.* (2001), who sampled mitochondrial DNA from six *Polyplectron* taxa but not *P. katsumatae* or *P. schleiermacheri*, found that Sumatran Peacock-Pheasant *P. chalcurum* is sister to *P. bicalcaratum*, and *P. inopinatum* is sister to these two. Like Collar (2009) they considered the phylogeny incongruent with the geographical implications, but lack of sampling of *P. chalcurum* by Chang *et al.* (2008) and of *P. katsumatae* by Kimball *et al.* (2001) make direct comparison of their results impossible. Another potential criticism of Chang *et al.* (2008) could be their failure to sample extensively across the range of mainland Asian *P. bicalcaratum*, as would be desirable to ensure that *P. katsumatae* is not nested within divergent mainland haplotypes of that species.

Our aims in this study were to resolve the species status and the closest relatives of *katsumatae* and *schleiermacheri*, and to determine the validity of doubts raised by Collar (2009) on the compatibility of molecular and morphological information.

Methods

We obtained fresh material of *P. katsumatae* and *P. schleiermacheri* (see Acknowledgements). The material of *P. katsumatae* was from the feather illustrated by Lee *et al.* (2005: Pl. 5). The material of *P. schleiermacheri* was from eggshell membranes, feathers and wet tissue of captives in Singapore, which showed no history or signs of hybridisation (L. K. C. Kuah pers. comm.). From AMNH we obtained wet tissue from a sample of *P. bicalcaratum* independent of those analysed by Chang *et al.* (2008), as well as a wet tissue sample of Crimson-headed Partridge *Haematortyx sanguiniceps*. We used the primers listed by Kimball *et al.* (1999) and Armstrong *et al.* (2001). We applied a DTT-based adaptation of the QIAGEN filter kit for extracting DNA from toepads and feathers of other taxa sampled via the Natural History Museum, Tring (BMNH), AMNH and Raffles Museum of Biodiversity Research, National University of Singapore (RMBR), including Painted Spurfowl *Galloperdix lunulata*, Germain's Peacock-Pheasant *P. germaini*, *P. chalcurum* and *P. inopinatum*. Cytochrome-*b*, D-loop and OvoG sequences were obtained by amplification, sequencing and overlapping partial sequences using the software SeqEdit (Applied Biosystems, USA). OvoG sequences (not obtained for *P. katsumatae* and *Haematortyx*) were aligned with Clustal X, this and other procedures being concordant with those used by Chang *et al.* (2008). We used these sequences to re-analyse a complete phylogenetic tree for all eight *Polyplectron* taxa, adding the GenBank information from the papers by Kimball *et al.* (2001) and Chang *et al.* (2008) for *Polyplectron* species, as well as cytochrome-*b*, D-loop and OvoG sequences from a range of taxa as outgroups. Phylogenetic trees were constructed using the maximum likelihood (ML) method implemented in PAUP* 4.0b10 (Swofford 1998) and a Bayesian tree was constructed using MrBayes software (http://mrbayes.sourceforge.net) at allcompat and halfcompat settings.

Like Collar (2009), we examined specimens of *P. katsumatae* in AMNH, and took notes on plumage and measurements. Because ocellus colours vary with angle of incident light, we viewed them all with the skin placed between the observer and light source, facing left. We supplemented these with notes on posture, plumage and bare-parts coloration from photographs of several live birds of both sexes in Li (2004) and Corder (2001), taken both

in the wild and at the South China Institute for Endangered Animals, Guangdong, China, by Y.-R. Gao.

We took notes on behaviour, plumage and voice of live captive *P. schleiermacheri*, and compared sonograms with closely related species, but were unable to obtain sound-recordings of *P. katsumatae*. Sonograms were prepared using Avisoft Sonagraph Pro developed by Raimund Specht, Berlin, with a software sampling rate of 16,000 Hz 16 bits, using a Soundblaster Audio Card (Creative Labs Inc) on an IBM compatible PC running Microsoft Windows.

Results

DNA.—Our results, shown in Figs. 1–2, were in full accord with those of Kimball *et al.* (2001) and Chang *et al.* (2008). Like Kimball *et al.* (2001) we found that *P. chalcurum* and *P. bicalcaratum* are sister taxa, and *P. inopinatum* is sister to this pair. Like Chang *et al.* (2008) we found that *P. katsumatae* is the next closest and that *P. germaini* is basal to all these preceding taxa. Our new material of *P. bicalcaratum*, *P. chalcurum*, *P. inopinatum*, *P. katsumatae* and *P. germaini* clustered respectively with the previously sequenced materials from each of these taxa. Although we had only one additional specimen of *P. bicalcaratum*, independent of those used by Kimball *et al.* (2001) and Chang *et al.* (2008), there is no evidence that any of these taxa (in particular mainland *P. bicalcaratum* vs. Hainan *P. katsumatae*) are paraphyletic.

We found that *P. schleiermacheri* was sister to *P. malacense*, and concurred with Kimball *et al.* (2001) and Chang *et al.* (2008) that Palawan Peacock-Pheasant *P. napoleonis* is basal to all congeners.

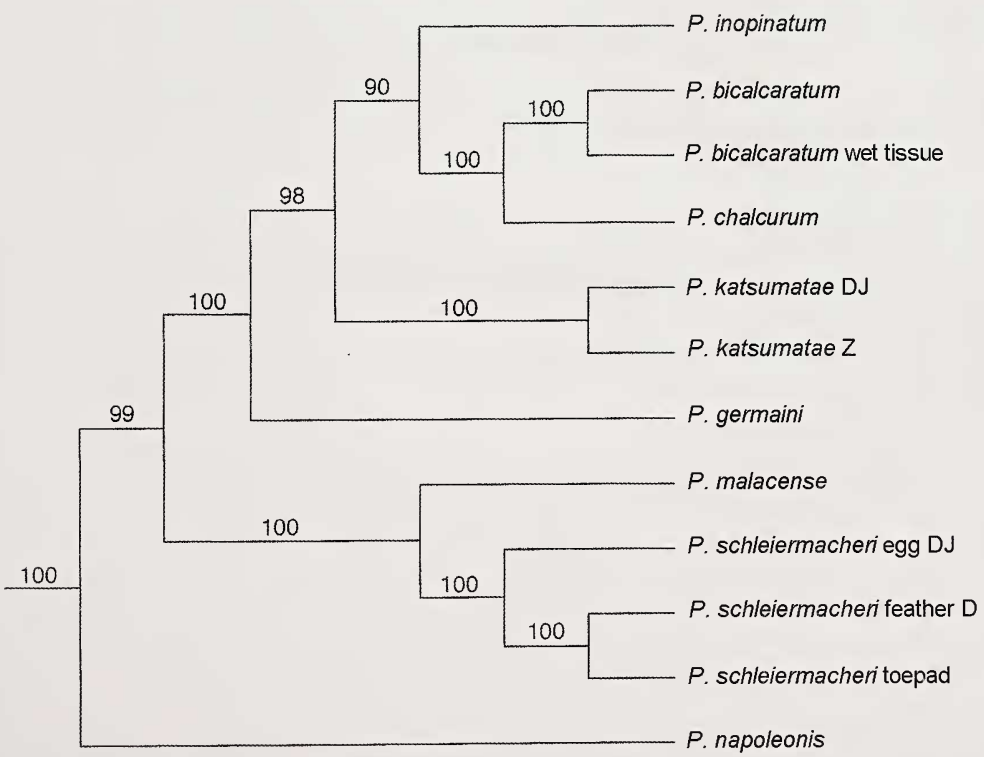

Figure 1. Consensus tree showing maximum likelihood (ML) values using all non-*Polyplectron* taxa as the outgroup and employing 50% majority rule bootstrap.

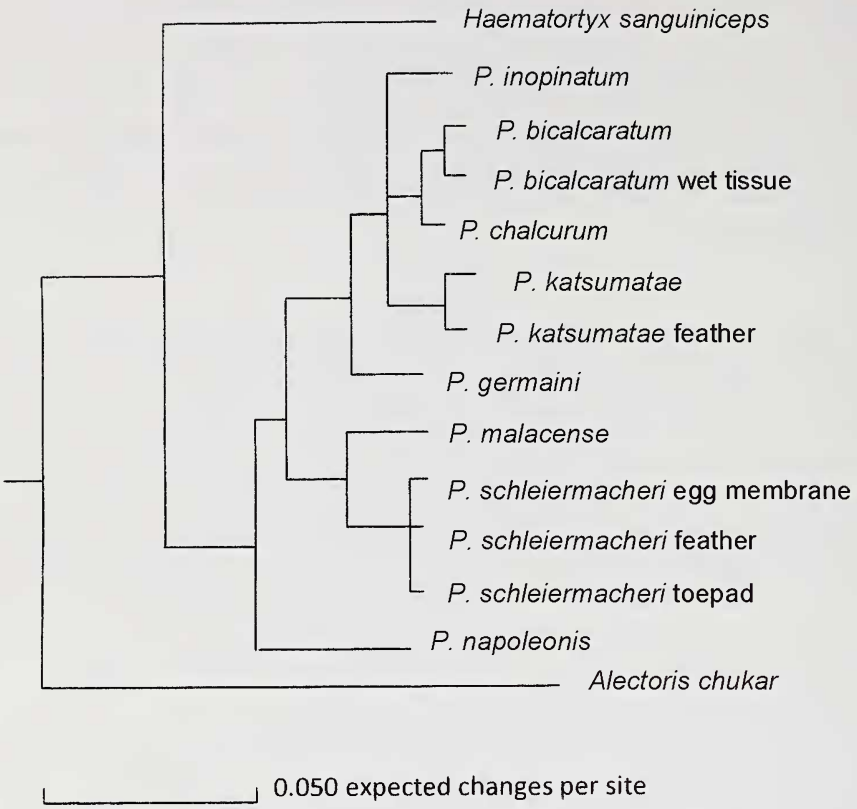

Figure 2. Phylogenetic tree created using MrBayes at halfcompat setting, rooted with *Gallus*, with branch length proportional to expected base changes per site.

Depending on the tree root, *Haematortyx* may be most closely related to *Polyplectron* (Fig. 2). We obtained short sequences from *Galloperdix lunulata*, too fragmentary for use in phylogenetic reconstruction and not differing from sequences in *Polyplectron*. All three genera have multiple spurs, and male *G. lunulata* has faint iridescence on the wing-coverts and tail, as well as white ocelli. Employment of different outgroups did not affect the topology of the *Polyplectron* clade, with the highly ornamented *P. napoleonis* always basal to other *Polyplectron*.

Plumage.—Five distinctions between *P. katsumatae* and *P. bicalcaratum* were listed by Collar (2009): remarkably smaller size; steel green (not steel purplish) ocelli on the wings and mantle; shorter crown feathers; crown darker than (not paler or uniform with) the neck and mantle; and darker body plumage as a result of much denser vermiculations. In addition we noted that the bare facial skin of live *P. katsumatae* is brilliant red, and this colour extends well behind the eye, and onto the mandible and maxilla as far as the anterior tip of the nares. The red colour extends over the operculum and can meet across the ridge of the culmen. The divide between bare facial skin and feathered supercilium is distinct and complete, whereas in *P. bicalcaratum* the facial skin bears numerous tiny feathers and there is very little bare skin posterior to the eye. In male *P. bicalcaratum* the bare skin ranges from dirty grey to pale yellow or buff, and extends to the base of the mandible but not the maxilla. Even if the colour variations in the bare skin of *P. bicalcaratum* are associated with

reproduction or hormonal change, the colour never reaches the intense red shown by *P. katsumatae*. Thus the colour, shape, extent and degree of bareness of the facial skin are all distinct. We found that one live female *P. katsumatae* had bare red facial skin and pale irides, whereas in female *P. bicalcaratum* the facial skin is sparsely feathered, grey to pale yellow or pinkish, and the irides brown.

We concur with Collar (2009) that the ocelli on the wings and mantle are steel green not steel purplish; the distinction is not subtle and it sorts all males of *P. katsumatae* from all those of *P. bicalcaratum*. In addition we note that the ocelli on the wings of *P. katsumatae* are broader than long and have a tiny distal point or 'tail' extending over the shaft. In both taxa the ocelli on the uppertail-coverts and rectrices are green, but they are brighter and greener in *P. katsumatae*. The ocelli on the rectrices of *P. katsumatae* are smaller, 17–21 mm max. length measured parallel to the shaft on the central rectrix (n = 4), compared with 24–27 mm in *P. bicalcaratum* (n = 4) and 19–21 mm in *P. germaini* (n = 4). The overall effect is of smaller ocelli, further from the tip of the tail (Table 1) but the blurred outline of the ocelli makes measurements imprecise.

TABLE 1
Ocellus dimensions in three taxa of *Polyplectron*. Each measurement refers to the maximum length of one ocellus on the outer web of a central rectrix of an individual male.

Length of ocellus (mm)	Distance to tip of rectrix (mm)	Ratio
P. katsumatae		
17	56	3.294
18	61	3.389
21	64	3.048
21	broken	–
P. bicalcaratum		
24	61	2.542
24	67	2.792
26	65	2.500
27	56	2.074
P. germaini		
19	58	3.052
21	65	3.095
21	48	2.286
21	62	2.952

In male *P. bicalcaratum* the ocelli on the inner and outer webs are separate on at least the inner 4–5 median tail-coverts. In male *P. katsumatae* the ocelli are fused at the shaft on all the median tail-coverts. Our impression is that more pairs of rectrices of male *P. bicalcaratum* have the ocelli separate (on 5–6 central pairs, and sometimes on all 10–12 pairs of rectrices), and this is true of fewer pairs of rectrices in male *P. katsumatae* (ocelli separate on 3–4 central pairs, never on all 9–10 pairs of rectrices) but that this is subject to much variation.

Collar (2009) noted that in body plumage *P. katsumatae* 'is somewhat darker, as a result of much denser vermiculations than *bicalcaratum*'. We add that these vermiculations are smaller, neater, rounder and more orderly, and less vermiform. We also found that both sexes are substantially browner, less grey, especially on the wings. Collar (2009) noted that the crown of *P. katsumatae* is darker, but we add that there is no iridescence on the crown or nape, a further distinction from *P. bicalcaratum*, which has purple iridescence on those feathers. In some features *P. katsumatae* resembles *P. germaini* (small size, red facial skin, darker and browner plumage) but in others it does not (pale iris, pale surrounds to ocelli).

In *P. schleiermacheri*, numerous major plumage distinctions from *P. malacense* have already been described and illustrated by Beebe (1922), Delacour (1951), Hennache & Ottaviani (2006) and others, including the short crest, pure white chin, white central breast stripe, black breast and flanks, iridescence at the breast-sides, transverse subterminal bars on the rectrices, and brilliant orange-red facial skin.

Voice.—Sonograms showed that the call of *P. schleiermacheri* differs from those of *P. napoleonis* and *P. malacense*. The call of *P. schleiermacheri* is an explosive high-pitched clarion with an almost quacking quality, usually consisting of two notes, *kank-kank*, but sometimes one *kank* per call, comprising broad frequency spectrum noise between 1.5 and 5.0 kHz,

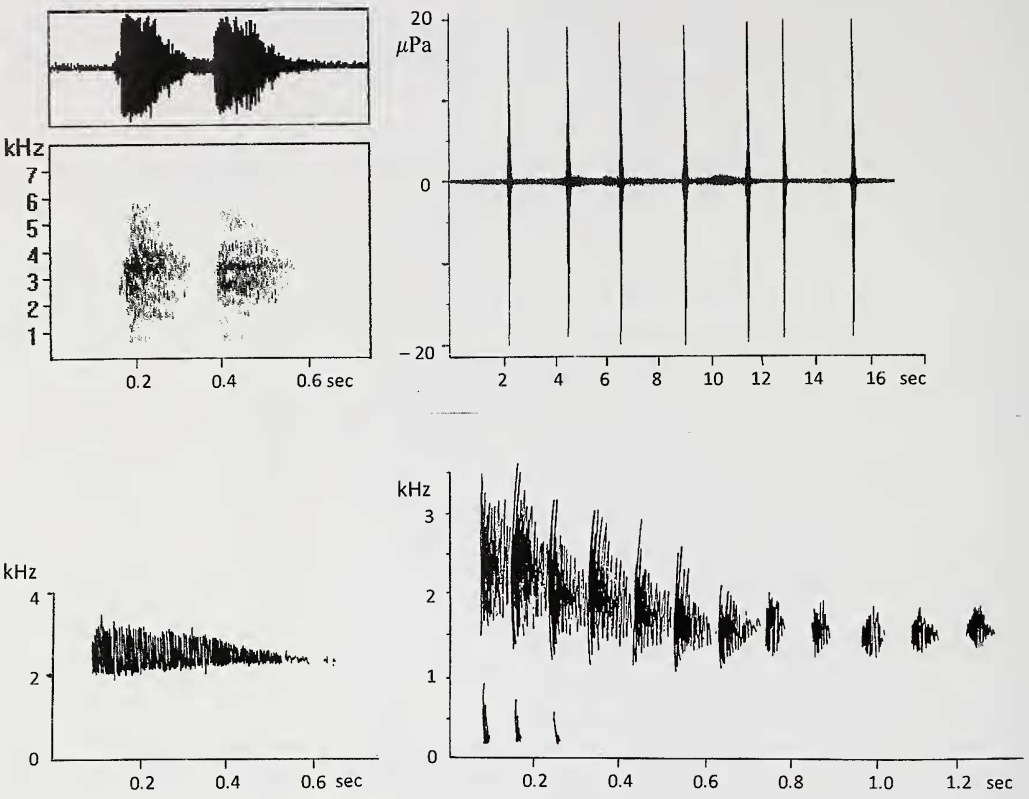

Figure 3 (upper left). Sonogram and pressure recording of two-note *kank-kank* advertising call of male *Polyplectron schleiermacheri* in captivity (GWHD: 20050618); (upper right) pressure recording of seven in a long series of single-note advertising calls of male *P. napoleonis* in captivity (GWHD: 20071104); (lower left) sonogram of single-note *tchorr* advertising call of male *P. malacense*, Pasoh, Negeri Sembilan, Malaysia (K. W. Scriven: 1969); (lower right) sonogram of long clucking series by male *P. malacense* that eventually degenerates to single *tchorr* calls, the series continuing for several minutes, Pasoh, Negeri Sembilan, Malaysia (K. W. Scriven: 1969).

with max. energy output around 3.5 kHz. Each note lasts *c*.0.15 seconds, and the duration of the two-note call is *c*.0.4 seconds. These calls are given every few seconds in a long series. Male *P. napoleonis* give higher pitched, more staccato, broad frequency spectrum single notes, each lasting *c*.0.15 seconds and given every few seconds in a long series at intervals of *c*.2 seconds. Max. energy output of 15–20 μPa is at a frequency around 3.5 kHz.

In addition to its soft, mellow, deliberate two-note pure whistle, male *P. malacense* gives single harsh notes (the *tchorr* call: Medway & Wells 1976); each note is a broad spectrum noise with max. energy output at around 2.5 kHz, with duration of 0.5 seconds (Fig. 3). Such notes are given at long intervals, but males sometimes deliver a long series of notes beginning with a single explosive *tchorr* tailing away into a prolonged chain of decelerating clucks (Fig. 3, lower right), repeated with progressively fewer clucks and greater emphasis on the first note at each repetition, until reaching a long series of spaced, single *tchorr* notes (Fig. 3, lower left). Such a progression in calling is unknown in *P. schleiermacheri* or *P. napoleonis*, but this could be due to shortage of field observations.

We could not be sure of comparing like with like, as the advertising *kank-kank* of *P. schleiermacheri* is distinct from both the advertising mellow whistle and harsh alarm *tchorr*

of *P. malacense*, but in captive *P. schleiermacheri* the call was used in aggressive and sexual contexts not alarm. There could be additional calls not yet known, but we could be sure that the known calls of *P. schleiermacheri*, *P. napoleonis* and *P. malacense* are all very different.

Discussion

There is now ample evidence from DNA sequencing and morphology that *P. katsumatae*, and from DNA sequencing, morphology and voice that *P. schleiermacheri*, are recognisable at species level. We have shown that there are numerous plumage and bare-parts distinctions between *katsumatae* and *bicalcaratum* additional to those listed by Collar (2009). The strong differences in facial skin colour and shape, ocellus colour and proportions that we noted in specimens are also clearly evident in photographs in Corder (2001), Li (2004) and Liang & Zhang (2011). The cumulative evidence from Kimball *et al.* (2001), Chang *et al.* (2008) and the present study shows that both taxa fully meet the Phylogenetic as well as the Biological Species Concept (BSC), using criteria described by Helbig *et al.* (2002), Parkin *et al.* (2006) and Tobias *et al.* (2010). Using the scoring system of Tobias *et al.* (2010), Collar (2009) scored *P. katsumatae* with seven out of a potential nine points, but the taxon might have scored even higher if a different set of morphological characters (e.g., the bare-part coloration less obvious in specimens) had been taken into account.

We cannot demonstrate failure to hybridise as a criterion for applying the BSC, as each taxon is allopatric in the wild and many Galliformes hybridise freely in captivity with intergeneric and even some interfamilial hybrids known (McCarthy 2006). But correlations between bare-part coloration and display features of *Polyplectron* are important in each species (Davison 1983); and the displays of *P. chalcurum* and *P. inopinatum*, which are located between *P. bicalcaratum* and *P. katsumatae* in the tree, are distinct in posture, movement and signal type (Davison 1985, 1992). We interpret this as strong evidence that each taxon studied here meets BSC criteria.

The finding by Chang *et al.* (2008) that *P. katsumatae* is not the sister taxon of *P. bicalcaratum* is additionally supported here, as both *P. chalcurum* and *P. inopinatum* show greater DNA sequence similarity to *P. bicalcaratum* than any of the three does to *P. katsumatae*. This is powerful evidence that *P. katsumatae* merits species rank. In contrast to Kimball *et al.* (2001) and Collar (2009) we do not consider this to be inconsistent with geography. On the contrary, expansion of an ancestral Asian mainland '*bicalcaratum*' down the western margin of the Sunda Shelf, during a drier period around the Pliocene–Pleistocene transition, would have been followed by the isolation of several peripheral populations caused by sea-level rise and higher rainfall. Speciation events were timed by Kimball *et al.* (2001) at 0.7 (0.2–1.2) MYA for *P. chalcurum*, 1.5 (0.8–2.2) MYA for *P. inopinatum*, and by Chang *et al.* (2008) at 1.4 (1.1–1.7) MYA for *P. katsumatae*. The broad margins of error, and possible differences in the rates of accumulation of differences in DNA sequences, are sufficient to allow for apparent discrepancies. For example, one would expect Sumatran *P. chalcurum* to have been isolated prior to or at the same time as Malay Peninsula *P. inopinatum*, and the margins of error given by Kimball *et al.* (2001) permit this. The picture is of a once more widespread mainland Asian taxon, from which peripheral populations were calved by one or a series of near-contemporaneous events, possibly speciation of *P. germaini* having been slightly the earliest and resulting in the form that was geographically least likely to mix with others (*chalcurum*, *inopinatum*, *katsumatae*) after isolation.

The first separation of Hainan from the mainland of southern China was *c.*2 MYA (Zhang 1999), followed by several episodes of unification during low sea-level glacials and separation during high sea-level interglacials. Pollen data from Hainan and mainland China (Zheng 2000, Lin & Zhang 2001) suggest the types of vegetation change these populations

would have experienced. Glacial events were accompanied by changes in rainfall on Hainan with the expansion of grassland, restriction of *Dacrydium*, *Castanopsis* and *Quercus* to upland forest, and increased abundance of *Mallotus* and *Casuarina* in the lowlands during drier glacial maxima (Zheng 2000), a pattern opposite to that on the mainland for which at least the Last Glacial Maximum was wetter.

This *Polyplectron* pattern is consistent with isolation of peripheral populations of other mainland Asian birds in western landmasses of the Sunda Shelf, e.g. Crested Argus *Rheinardia ocellata*, Hill Prinia *Prinia atrogularis* and Black-throated Sunbird *Aethopyga saturata* in the Malay Peninsula, and Grey-headed Woodpecker *Picus canus* in the Malay Peninsula and Sumatra. It is not our purpose to put a case for the dating of range extensions by these birds, merely to point out biogeographical parallels. We envisage that for *Polyplectron* such events would have occurred when other lowland *Polyplectron* were confined to a moister eastern or central block of the Sunda Shelf, *P. napoleonis*, *P. schleiermacheri* and *P. malacense* representing successive differentiation of populations from east to west and isolating *P. inopinatum* in the mountains of the Malay Peninsula as wetter conditions permitted the spread of *P. malacense* and the retreat of '*bicalcaratum*' in the lowlands.

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